





## Subtle changes in elevation shift bat-assemblage structure in Central Amazonia

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### ABSTRACT

The distribution patterns of animal species at local scales have been explained by direct influences of vegetation structure, topography, food distribution, and availability. However, these variables can also interact and operate indirectly on the distribution of species. Here, we examined the direct and indirect effects of food availability (fruits and insects), vegetation clutter, and elevation in structuring phyllostomid bat assemblages in a continuous *terra firme* forest in Central Amazonia. Bats were captured in 49 plots over 25-km<sup>2</sup> of continuous forest. We captured 1138 bats belonging to 52 species with 7056 net\*hours of effort. Terrain elevation was the strongest predictor of species and guild compositions, and of bat abundance. However, changes in elevation were associated with changes in vegetation clutter, and availability of fruits and insects consumed by bats, which are likely to have had direct effects on bat assemblages. Frugivorous bat composition was more influenced by availability of food-providing plants, while gleaning-animalivore composition was more influenced by the structural complexity of the vegetation. Although probably not causal, terrain elevation may be a reliable predictor of bat-assemblage structure at local scales in other regions. In situations where it is not possible to collect local variables, terrain elevation can substitute other variables, such as vegetation structure, and availability of fruits and insects.

Abstract in Portuguese is available with online material.

*Key words:* bat assemblages; Chiroptera; diversity; environmental filter; environmental heterogeneity; food availability; topography; vegetation structure.

SPECIES ARE NOT RANDOMLY DISTRIBUTED, AS THEY PERCEIVE THE ENVIRONMENT AS gradients in resource availability and seek areas with better chances to find food, shelter, and breeding sites. Variation in habitat types, food resources, and refuges increases the number of niches available and allows for more species to coexist (Kerr & Packer 1997, Stein *et al.* 2014), thereby increasing the number of species and playing an important role in structuring communities (Stein *et al.* 2014, Jiménez-Alfaro *et al.* 2016).

At local geographic scales, vegetation (*e.g.*, cover and structure), topography, and soil variation are factors that often explain terrestrial animal distributions (Hortal *et al.* 2013, Stein *et al.* 2014). The influence of vegetation may result from variation in physical structure and plant taxonomic composition, which affects the availability of food and shelter and constrains movement (Castagneyrol & Jactel 2012, Whitfeld *et al.* 2012, Oliveira *et al.* 2015, Bobrowiec & Tavares 2017). Resource distributions

are strongly related to topography. Regions with large elevational changes (>3000 m) have large soil, climate, and vegetation gradients, which create multiple habitat types that promote species turnover (McCain 2007, Willig & Presley 2016). However, subtle changes in elevation (<100 m) may also affect species distributions (Menin *et al.* 2007, Fraga *et al.* 2011, Cintra & Naka 2012, Baccaro *et al.* 2013, Dias-Terceiro *et al.* 2015) and may be correlated with water table depth, temperature, soil fertility and texture, which promote changes in plant species composition (Pansonato *et al.* 2013, Schiatti *et al.* 2014).

The variables that determine the patterns of animal diversity might also operate indirectly by changing other predictor variables that directly shape species distribution. In *terra firme* forests, lower elevation areas are usually associated with nutrient-poor sandy soils and small streams (Costa *et al.* 2009, Pansonato *et al.* 2013). Plant populations respond to soil characteristics and to the height of the water table, forming different plant assemblages along the edaphic gradient. Therefore, terrain elevation may be used as a surrogate for changes in plant-assemblage composition (Moulatlet *et al.* 2014, Schiatti *et al.* 2014). As herbivorous insects

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often consume specific plant genera or species (Haddad *et al.* 2009, Müller & Brandl 2009), differences in terrain elevation will indirectly affect herbivorous insect assemblages (Jayapal *et al.* 2009, Jankowski *et al.* 2013). The physical structure of vegetation is also determined by the plant-assemblage composition and indirectly by elevation (Castilho *et al.* 2006, Oliveira *et al.* 2015). Vegetation tends to be more open in areas around small streams compared to more cluttered terrestrial habitats. Open areas allow easier movement of animals, in particular volant species, such as birds and bats (Bueno *et al.* 2012, Bobrowiec & Tavares 2017). Thus, we hypothesise that terrain elevation shows strong correlation with other predictors, such as food availability (fruits and insects) and vegetation clutter, and can be used as a proxy for edaphic gradients that affect animal diversity at local scales.

Bats are suitable models to study the effects of environmental heterogeneity because of the high number of species and well-known foraging guilds (Bobrowiec *et al.* 2014, Farneda *et al.* 2015, Rocha *et al.* 2017). Bats respond to altitudinal gradients (Bobrowiec & Tavares 2017), climate (Estrada-Villegas *et al.* 2012), and their occurrence and relative abundance are directly related to vegetation structure (Bobrowiec *et al.* 2014, Bobrowiec & Tavares 2017, Rocha *et al.* 2017). Frugivorous and nectarivorous bats are directly influenced by the diversity of plants because of constraints related to the availability of fruits and flowers (Marques *et al.* 2012). The composition of assemblages of insectivorous bats can also be directly associated with vegetation structure and plant diversity (Dodd *et al.* 2008, Jung *et al.* 2012). Bat foraging guilds interact in different ways with the physical structure of vegetation (Marciente *et al.* 2015, Bobrowiec & Tavares 2017). Gleaning animalivores are more generalist and use environments with different levels of vegetation clutter, while canopy frugivores are more common in sites with more open vegetation (Marciente *et al.* 2015).

Although topography, vegetation structure, and food availability have been implied as predictors of bat community structure (Marques *et al.* 2012, Marciente *et al.* 2015, Bobrowiec & Tavares 2017, Rocha *et al.* 2017), few studies in Amazonia have attempted to test their effects on species distributions and to test possible direct and indirect effects of these variables. In this study, we aimed to distinguish the direct and indirect effects of topography, vegetation structure, and food quantity and composition as predictors of bat distribution patterns and assemblage structure. We analyze direct and indirect effects of these variables on different components of bat taxonomic diversity (number of species, abundance, and species composition) in an area covering 25-km<sup>2</sup> of continuous forest in Central Amazonia. We predicted that vegetation clutter and food availability would contribute directly to explain the bat guild distribution and assemblage structure, and that terrain elevation could be used as an indirect surrogate for these variables. We also expected that food availability would be positively associated with abundance of species in different guilds and that the physical obstruction by vegetation would reduce the number of bat species and their abundance, but with a lesser impact on gleaning animalivorous bats.

## METHODS

**STUDY AREA.**—We conducted the study in Reserva Florestal Adolpho Ducke (02°55′–03°01′ S; 59°53′–59°59′ W; Ducke Reserve hereafter), located on the outskirts of Manaus (Km 26 on the AM-110 Highway, Amazonas State, Brazil—Fig. S1). The reserve is included in the Long-term Ecological Research Program of the Brazilian National Research Council (Programa de Pesquisas Ecológicas de Longa Duração—PELD/CNPq) and harbors 10,000 ha of mature *terra firme* forest. The dry season generally occurs from June to October and the rainy season from November to May. Annual rainfall in 2013 was 3385 mm and mean daily temperature was 24.9 °C (data from Ducke Reserve Climatological Station). Forest canopy in the reserve ranges from 30 to 35 m high and emergent trees reach up to 50 m (de Oliveira *et al.* 2008). The relief is irregular, with altitudinal variation of 62.3 to 123.9 m (mean ± SD; 94.8 ± 20.1 m; Ribeiro *et al.* 2002).

A trail system forming a 25-km<sup>2</sup> grid (5 × 5 km) according to RAPELD method (RAP = rapid survey of biological communities; PELD = long-term ecological research; Magnusson *et al.* 2005) was used in this study (Fig. S1). The grid has 30 permanent plots systematically spaced at 1 km intervals (de Oliveira *et al.* 2008), five of which are in riparian areas close to watercourses. Additionally, 19 riparian plots are placed parallel to watercourses, totaling 49 sampling plots (24 riparian and 25 non-riparian plots; Fig. S1). Each plot was 250 m long and 40 m wide and systematically spaced plots followed the topographic contour to minimize internal heterogeneity in soil properties and drainage. Riparian plots follow the stream gradient, which is very shallow in this region (Magnusson *et al.* 2014).

**BAT CAPTURES.**—We captured bats using eight ground-level mist nets (12 × 3 m, 19 mm mesh, Ecotone<sup>®</sup>, Poland) per plot (Fig. S2) between October 2013 and February 2014. Each plot was sampled on three non-consecutive nights, totaling 7056 net-hours (1 net-hour = one net open for one hour). Nets remained open between 1800 and 0000 h, and were checked every 15 min. Each captured bat was identified and allocated to a foraging guild based on the literature reports of habitat use, foraging mode, and echolocation behavior (Kalko 1998). We used the categories gleaning animalivores, frugivores, aerial insectivores, nectarivores, and sanguivores. Bat identifications were based on the dichotomous keys of Lim and Engstrom (2001), and the descriptions of Simmons and Voss (1998), Charles-Dominique *et al.* (2001), and Gardner (2007). Taxonomy follows Gardner (2007) with modifications by Nogueira *et al.* (2014).

**ESTIMATES OF FRUIT AND INSECT AVAILABILITY.**—We estimated fruit availability for frugivorous bats by comparing the list of plant genera with fruits consumed by bats from Brazil compiled by Bredt *et al.* (2012), with the list of plant genera recorded in each plot available on the PPBio data base (<http://peld.inpa.gov.br/knb/metacat/melo.62.9/peld> and <http://peld.inpa.gov.br/knb/>

metacat/fecosta.55.3/peld) to produce a list of potential plant genera consumed by bats in each plot. We used this list to actively search for plants with fruits in areas of 1500 m<sup>2</sup> (6 × 250 m) on both sides of the central line of each plot (Fig. S2). We visited each plot three times during daylight hours on the days preceding the nocturnal netting sessions to find plants of the given genera with available fruits on the same night as bat captures. Plants with fruits were identified to the genus level, and fruit availability was quantified as the number of plants with fruits per plot.

We quantified insect availability as the mass of insects collected by light traps, which consisted of 20 cm diameter cones inserted in plastic pots of 100 ml containing a 70% alcohol solution and detergent. A flashlight with 10 white LED bulbs pointed at the cone was set above the cone to attract insects, which were retained in the plastic pot. We installed two light traps in each plot, positioned at 65 and 130 m distant from the closest mist net and along the central line of the plot (Fig. S2) and placed at a height of 1.5 m from the ground. The distances between the nets and the insect traps minimized the capture of insectivorous bats attracted to the light traps. We turned on the light traps at 1800 h on bat capture nights and turned them off after 48 h. Light traps functioned during the day and night, but probably attracted insects only at night. Each plot was sampled during two days three times, totaling 28224 trap-hours (1 trap-hour = one trap lit for one hour). Collected insects were dried on filter paper to remove excess alcohol and weighed individually on a precision balance (limit of reading 0.0001 g; Ohaus Discovery, Pine Brook, New Jersey). To estimate the total mass of insects collected in each plot, we combined the six insect-sampling nights of each plot. We identified the insects to the level of order.

**UNDERSTORY VEGETATION CLUTTER.**—We followed the methods proposed by Marsden *et al.* (2002) to measure vegetation clutter, with the modifications proposed by Oliveira *et al.* (2015). We took digital photographs of a 3 × 3 m white cloth panel placed at intervals of 10 m along a 250 m stretch of the central line of the plot ( $N = 25$  vegetation photographs per plot). The camera was positioned eight meters from the cloth panel, and oriented parallel to the central line of the plot, perpendicular to the panel. We converted photographs to black (vegetation) and white, and estimated the percentage of the black portion from the 25 photographs using the Sidelook 1.1.01 software (Zehm *et al.* 2003). We then summed the black areas of all 25 photos from each plot to quantify the percentage of area covered by vegetation.

**TOPOGRAPHY.**—We extracted the terrain elevation data for each plot from Shuttle Radar Topographic Mission (SRTM) in 90 m resolution rasters images provided by The Global Land Cover Facility (<http://www.landcover.org>). The geographical coordinates used to obtain terrain elevations were measured at the midpoint of each plot, and we used the ‘Point sampling tool’ from 2.2.0 Valmiera Quantum Geographic Information System software (QGIS) to extract the elevation values.

**DATA ANALYSIS.**—We included only phyllostomid bats in the analyses, because of the bias introduced using mist nets to sample other bat families (Kalko 1998). All raw data related to bats, elevation, vegetation clutter, plants and insects sampled can be accessed at the of PPBio public repository (<http://ppbio.inpa.gov.br/repositorio/dados>) by the title in Portuguese ‘Morcegos, altitude, frutos e insetos em 49 parcelas da Reserva Florestal Adolpho Ducke’.

We calculated direct and indirect effects of predictor variables using structural equation modeling (SEM) with the *sem* package (Fox 2017). We built 13 path diagrams for the following response variables: total number of species, total abundance, species and guild composition, number of species, abundance and species composition of each guild. We included only gleaning animalivores, frugivores, and nectarivores in the analyses. The predictor variables were understory vegetation clutter, terrain elevation, and food availability and composition (insects for animalivorous species and fruits for frugivorous and nectarivorous species).

We used a one-dimensional non-metric multidimensional scaling (NMDS) ordination to represent the species, guilds, and intra-guild composition, based on the Bray–Curtis dissimilarity index on abundance data. All NMDS ordinations were run using the *vegan* package (Oksanen *et al.* 2014) with metaMDS function ( $k = 1$ , trymax = 5000), in R 2.15.0 (R Core Team 2014).

We estimated food availability for frugivorous bats by counting the number of plants with fruits potentially consumed by bats. The fruit composition was also represented by a one-dimensional NMDS ordination, using the abundance of fruiting plants available to bats. Similarly, we estimated the food availability for insectivorous bats by the mass of insects (in grams). Insect composition was represented by a one-dimensional NMDS ordination using the abundance of insect orders. In both cases, we used the Bray–Curtis dissimilarity index.

Insects mass and insect order composition were included in SEM models as predictor variables along with the response variables number of species, abundance, and species composition of gleaning animalivorous bats. The number of plants with fruits potentially eaten by bats and plant composition was used as predictor variables in the SEM models with the response variables number of species, abundance, and species composition of frugivorous and nectarivorous bats. Elevation and vegetation clutter were included as predictor variables for all 13 SEM models.

We used only logical interactions between pairs of predictor variables in SEM models, rather than all possible interactions between pairs of predictor variables, and all relationships were unidirectional. Standardized path coefficients indicate the direction (+ or –) and the magnitude of the effect of a variable on the other variable with all other variables held constant (Mitchell 1992). Path coefficients between 0.25 and 0.50 were considered to be moderately strong, and those >0.5 were considered strong. Before running the SEM models, we initially evaluated the multicollinearity between pairs of predictor variables using a Pearson’s correlation test. All the correlations between pairs of predictor variables were weak ( $r \leq 0.40$ ), and no variable was removed.

## RESULTS

We captured 1138 bats, belonging to 52 species and five families (Table S1). Most individuals and species captured belonged to the family Phyllostomidae (1062 bats; 39 species), which represented 93% of all captures and 75% of all species. Only five species, all phyllostomids, occurred in over half of the plots, and only *Carollia perspicillata* occurred in all plots. Ten species occurred only in one (eight species) or two (two species) sampling plots (Table S1). Frugivorous bats were most commonly captured, with 770 captures and 16 species, followed by gleaning animalivores ( $N = 180$ ; 16 species), nectarivores ( $N = 111$ ; 6 species), aerial insectivores ( $N = 76$ ; 13 species), and a single blood-feeding bat.

We recorded 173 fruiting plant individuals from 12 genera that were potentially consumed by frugivorous bats (Table S2). The number of plants with fruits per plot ranged from 0 to 12 (mean  $\pm$  SD;  $2.4 \pm 3.5$ ), and the number of genera varied from 0 to 5 ( $2.2 \pm 1.2$ ). Four plots had no fruit for bats. We collected 11064 insects from 21 orders (Table S3). The number of orders recorded in each plot ranged from 4 to 15 ( $7.93 \pm 2.32$ ) and the total mass of insects per plot varied from 0.1 to 13.07 g ( $3.3 \pm 3.0$  g). Vegetation clutter ranged from 47% to 69% ( $57.4 \pm 5.9\%$ ) and terrain elevation varied from 56 to 124 m ( $82.2 \pm 20.1$  m).

Elevation was the predictor variable with the highest direct contribution to species composition (standardized path coefficient =  $-0.37$ ), guild composition ( $-0.39$ ), frugivore ( $0.37$ ), and nectarivore species composition ( $0.52$ ) (Figs. 1 and 2). The abundance of all phyllostomid species (Fig. 1) and of frugivores (Fig. 2A) decreased and the number and abundance of animalivorous species (Fig. 2C) increased in more elevated plots. This result occurred because *Carollia benkeithi*, *D. gnoma*, *Vampyriscus bidens*, *A. caudifer*, and *Hsunnycteris thomasi* were more captured in lower elevation plots, while *Artibeus planirostris*, *Micronycteris hirsuta*, *M. microtis*, and *Mimon crenulatum* occurred mainly in more elevated areas (Fig. 3). *Rhinophylla pumilio*, *Tonatia saurophila*, *Trachops cirrhosus*, *P. elongatus*, *C. brevicanda*, and *C. perspicillata* occurred over the entire elevational gradient (Fig. 3).

Elevation also contributed indirectly to the composition of frugivorous ( $-0.40$ ; Fig. 2A) and nectarivorous species ( $-0.31$ ; Fig. 2B) because of its effect on fruit composition. The plants *Henriettea*, *Piper*, and *Bactris* were more frequently encountered in the elevated plots, and *Peperomia* and *Clidemia* were more frequent in the lower plots (Fig. S3). Fruit composition was the only predictor variable related to food resources that influenced the composition of frugivorous and nectarivorous species.

The composition of animalivorous species was directly affected by vegetation clutter  $-0.27$ ; Fig. 2C), which in turn was related to elevation ( $0.30$ ). Overall, the vegetation was more open and less cluttered in the lower plots than in the plots located on plateaus. There was a direct and positive relationship of elevation with other predictors, such as the number of fruit trees ( $0.30$ – $0.33$ ), insect mass ( $0.34$ – $0.44$ ), insect composition ( $0.26$ – $0.27$ ; Fig. S4), and vegetation clutter ( $0.30$ – $0.41$ ), but the contribution

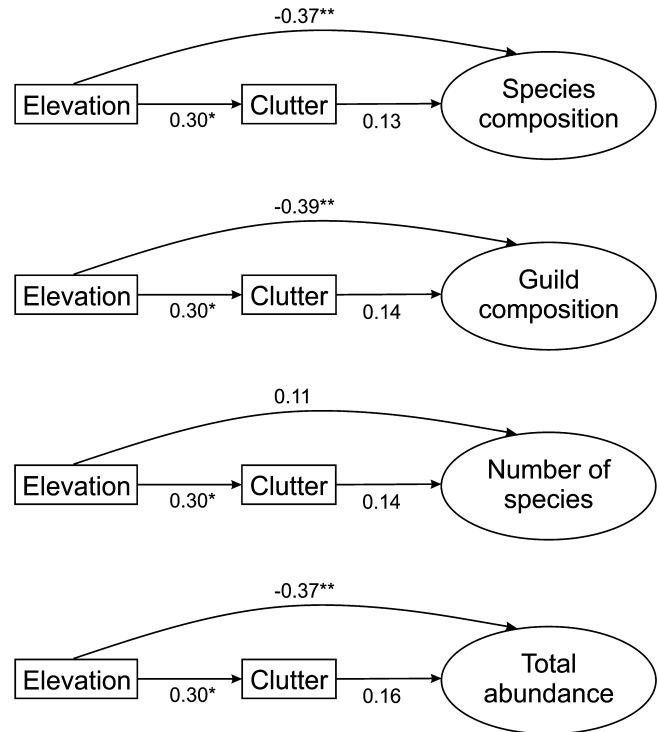


FIGURE 1. Standardized effects obtained by structural equation modeling for explaining bat diversity variables. Predictor variables were understory vegetation clutter (Clutter), and terrain elevation (Elevation). Species and guild composition, total number of species and total abundance represent response variables (in ovals) and boxes represent predictor variables. Coefficients between 0.25 and 0.50 are considered moderately strong. Significance level:  $*P < 0.01$ ,  $**P < 0.001$ ,  $***P < 0.0001$ .

of these predictor variables to bat diversity in most cases was weak (Figs. 1 and 2).

## DISCUSSION

We found that elevation plays a key role in structuring bat assemblages at the Ducke Reserve. A small change of 67.4 m in terrain elevation estimated by SRTM (min = 56.4 m, max = 123.9 m) affected number of bat species, abundance, and species and guild composition. These results are consistent with previous studies of bats (Bobrowiec & Tavares 2017), ant communities (Vasconcelos *et al.* 2003), other mammals (Rickart 2001), birds (Cintra *et al.* 2006, Bueno *et al.* 2012), and frogs (Menin *et al.* 2007, Rojas-Ahumada *et al.* 2012).

As predicted, the elevation was associated with variation in vegetation structure and thereby influenced the distribution of fruits and insects potentially consumed by bats. In Ducke Reserve, terrain elevation influences soil texture, which in turn is related to palm and shrub species composition (Kinupp & Magnusson 2005, Rodrigues *et al.* 2014) and to the woody vegetation structure (Castilho *et al.* 2006). The soils are more sandy and waterlogged in lower areas, but have a more clayey texture on the

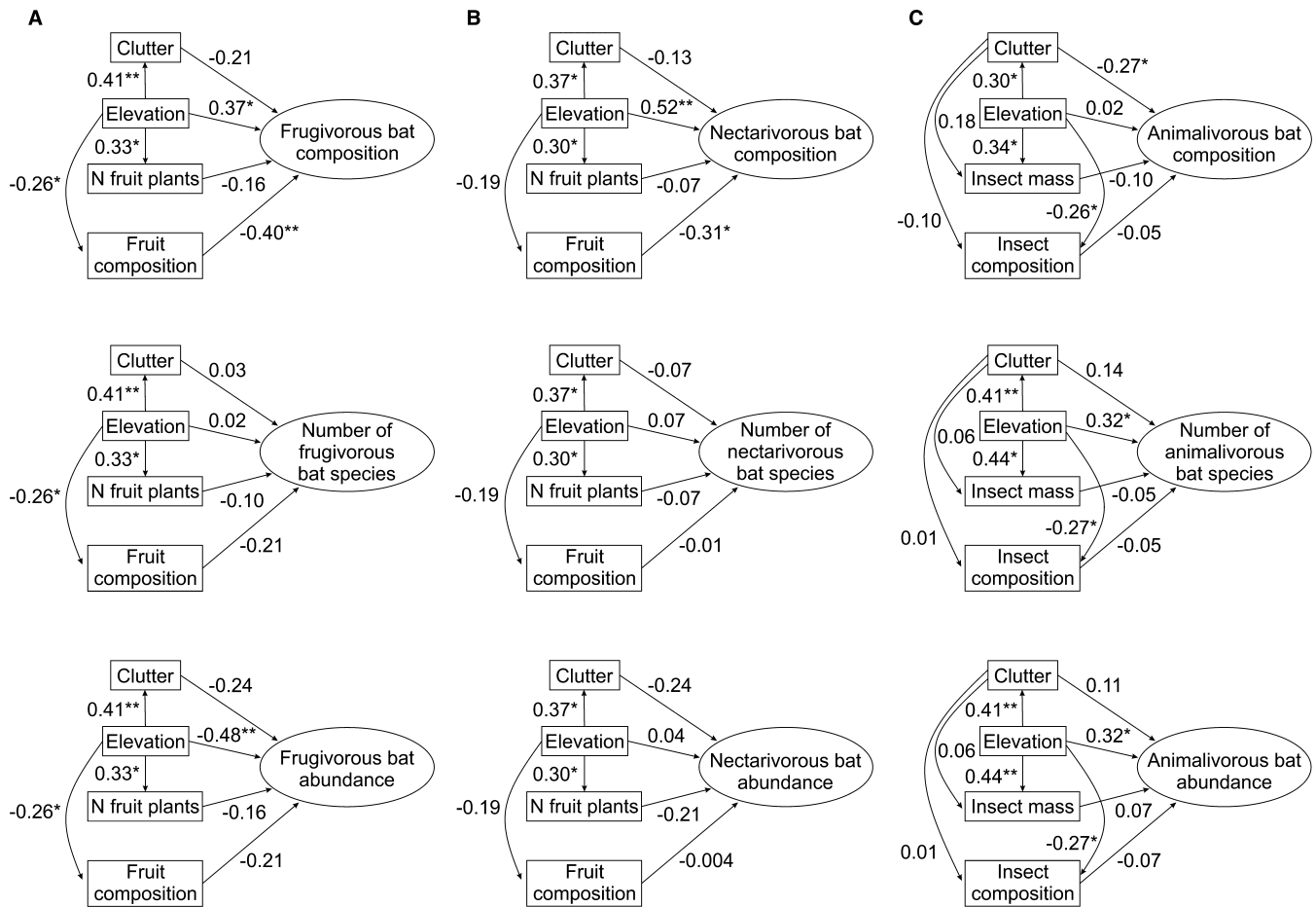


FIGURE 2. Results for the structural equation models for explaining species composition, number of species, and abundance of (A) frugivorous, (B) nectarivorous, and (C) gleaning animalivorous bats. Predictor variables were understory vegetation clutter (Clutter), terrain elevation (Elevation), number of plant genera with fruits consumed by bats (N fruit plants), a one-dimensional NMDS ordination axis of the plant genera consumed by bats (Fruit composition), insect mass (Insect mass), and a one-dimensional NMDS ordination axis of insect orders (Insect composition). Bat diversity was the response variable (in an oval) and boxes represent predictor variables. Coefficients between 0.25 and 0.50 are considered moderately strong, and those  $>0.5$  are considered strong. Significance level:  $*P < 0.01$ ,  $**P < 0.001$ ,  $***P < 0.0001$ .

plateaux (Chauvel *et al.* 1987, Costa *et al.* 2005). Shrubs and palms are important sources of food for frugivorous and nectarivorous bats, and assemblages of these plant taxa are related to the elevation gradient at the Ducke Reserve (Raupp & Cintra 2011, Rodrigues *et al.* 2014, Freitas *et al.* 2016). Abundance and number of species of gleaning animalivorous bats were higher on the plateaux, which are areas more distant of the streams. Small forest streams can be considered as clearings because they have more open vegetation (Oliveira *et al.* 2015). As gleaning animalivores avoid open areas and forest edges (Meyer & Kalko 2008), it is possible that this guild also avoids foraging along streams where the canopy is more open.

Our results showed that the plant species consumed by bats were more strongly associated with the distribution of frugivorous species than the number of plants bearing fruits, indicating that selected foraging areas for frugivores may be more strongly limited by the distribution of fruit-providing species than by the

amount of fruits available on a given night. Some frugivorous species appeared to have their distributions associated with areas where specific fruits occurred, which in turn was related to the elevational gradient. The bats *D. gnoma* and *R. fischeriae* were more abundant in the lower plots that contained *Clidemia* and *Peperomia*, while the three large *Artibeus* (*A. lituratus*, *A. obscurus*, and *A. planirostris*) were more frequent on the plateaux with a higher abundance of *Bactris*, *Henriettea*, *Oenocarpus*, and *Philodendron* (Fig. 4). The fruits of *Peperomia*, *Bactris*, *Oenocarpus*, and *Philodendron* are known to be consumed by species of the genera *Artibeus*, *Dermaptera*, and *Rhinophylla* (LoGiudice & Ostfeld 2002, Bredt *et al.* 2012, Marques *et al.* 2012) and may have influenced their distribution. The three species of *Carollia* are known to feed preferentially on Piperaceae fruits (Andrade *et al.* 2013). These bats were associated with *Peperoma* distribution, but contrary to what we expected, the distribution of *Carollia* at the Ducke Reserve had little relationship to the distribution of *Piper* plants, a genus of

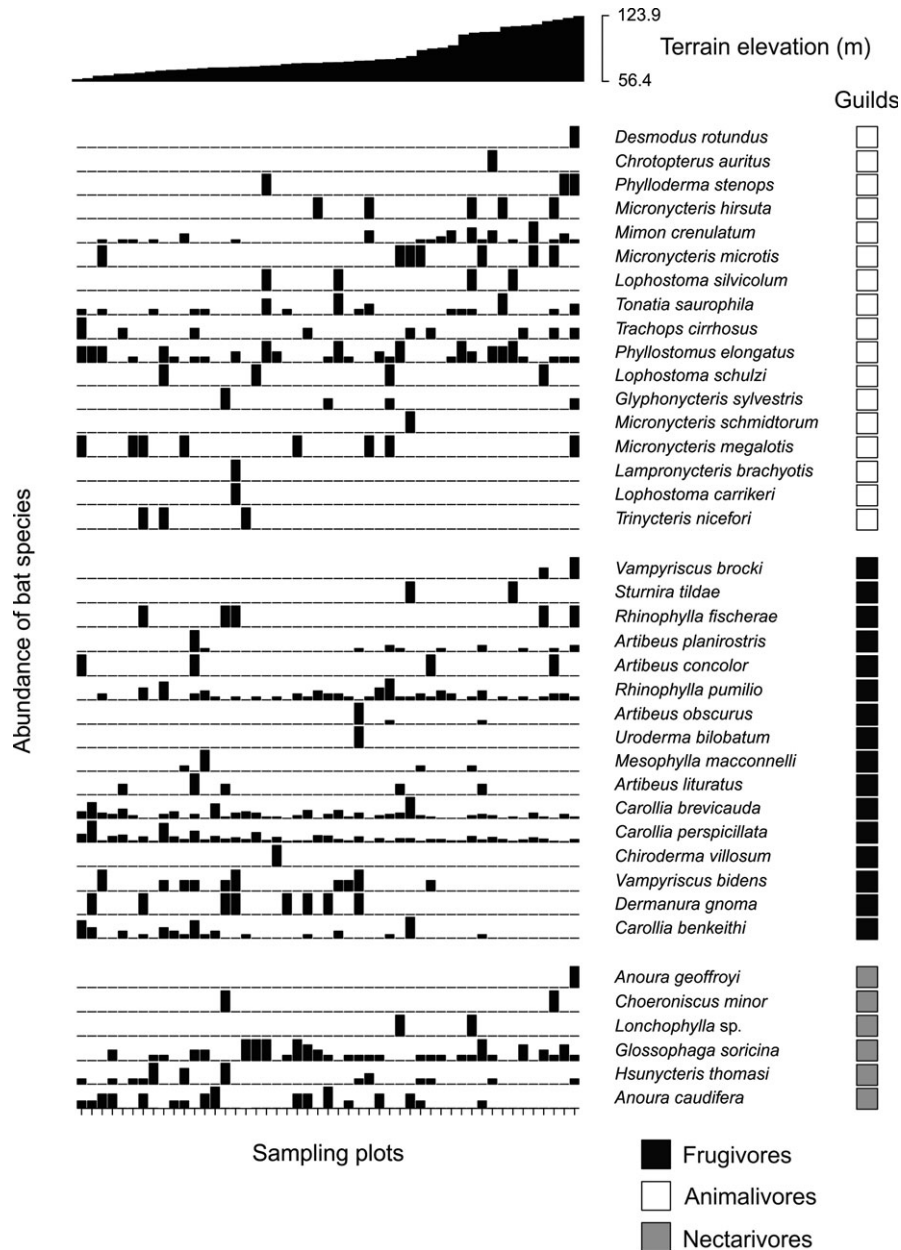


FIGURE 3. Bat abundance distribution along the gradient in terrain elevation at Ducke Reserve. The horizontal order of the sampling modules was based on the gradient in terrain elevation. The vertical order of bat species within each guild was based on the mean terrain elevation at which the species occurred weighted by abundance. Bat species more abundant on the plateaus within each guild are placed more to the right side of the graph and bats more abundant in plots located in lower areas are positioned to the left.

Piperaceae that is more common than *Peperoma* (Fig. 4). This indicates that there may be other factors besides food availability influencing the distribution of *Carollia* in Ducke Reserve.

Vegetation structure has been related to the organization of bat assemblages at wide and local scales in Central Amazonia (Marciente *et al.* 2015, Bobrowiec & Tavares 2017). The use of cluttered environments varies among bat guilds (Marciente *et al.* 2015, Bobrowiec & Tavares 2017), and is associated with foraging modes and differences in wing morphology and echolocation

characteristics (Stockwell 2001, Siemers & Schnitzler 2004). Frugivorous bats have wings adapted to move over considerable distances in search of food which occurs in patches (Bonaccorso & Gush 1987, Lobova *et al.* 2009), and these species tend to use more open areas within the forest (Bobrowiec *et al.* 2014, Marciente *et al.* 2015). Gleaning animalivores have wings adapted for slower flight and higher maneuverability (Norberg & Rayner 1987), and are more tolerant of highly cluttered environments (Marciente *et al.* 2015). The extent of vegetation clutter in Ducke

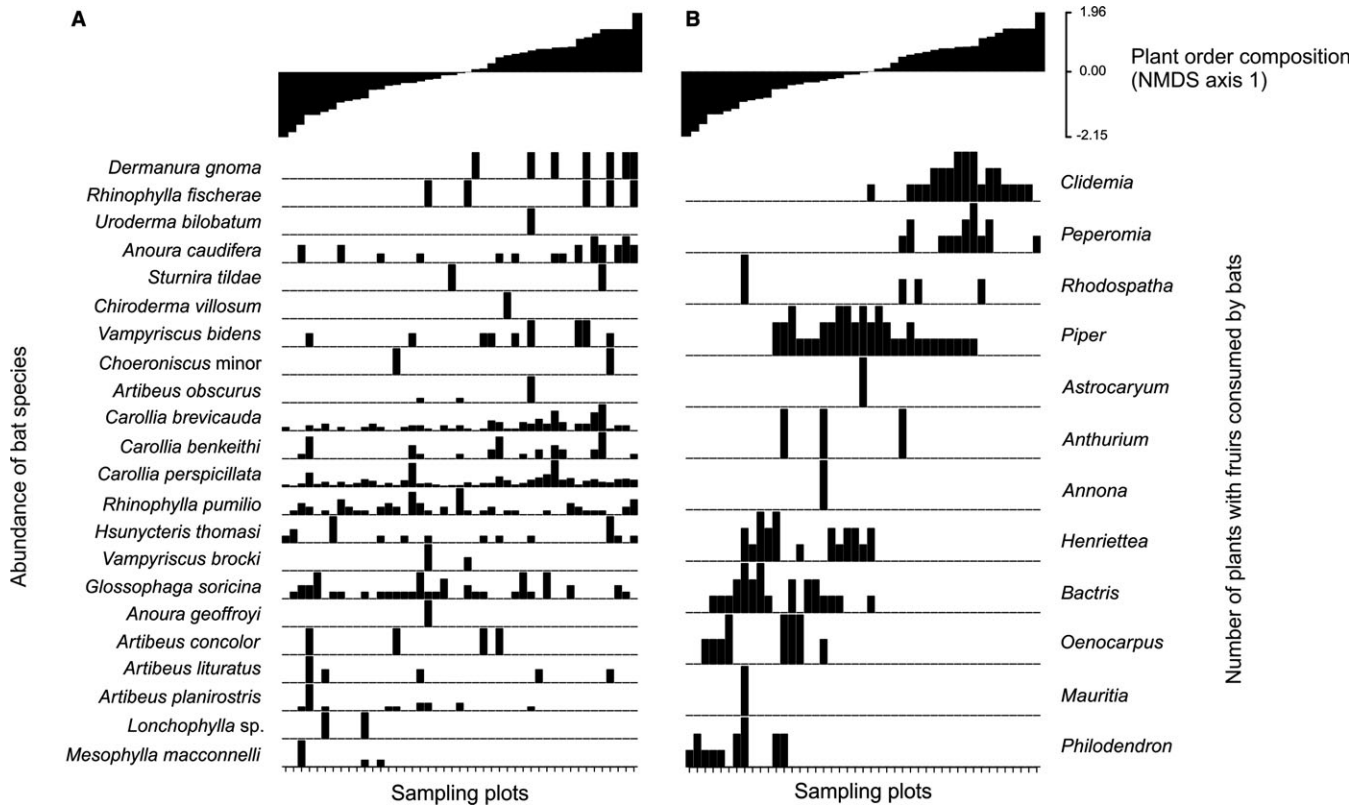


FIGURE 4. Distribution of frugivorous and nectarivorous species abundance (A) and abundance of plants with fruits consumed by bats (B) in relation to a one-dimensional NMDS axis of plant genera composition. As the two distributions are ordered by the same variable (NMDS axis 1 of the plant genera), the horizontal order of the sampling modules is the same for the two graphs.

Reserve was related to the composition of gleaning animalivorous species, indicating that vegetation in the Ducke Reserve is dense enough to constrain this guild. Although the plot vegetation did not directly affect the frugivorous and nectarivorous bats, these guilds were related to lower areas near streams where the vegetation is more open (Oliveira *et al.* 2015). Small streams form tunnels within the forest with fewer obstacles for bats, allowing them to move between areas at lower energy cost (Hagen & Sabo 2011).

Contrary to our predictions, neither insect composition nor insect mass appeared important in structuring the gleaned animalivorous bat assemblages, probably because the availability of insects is more unpredictable in space than the availability of fruits (Jones & Rydell 2003, Dechmann *et al.* 2011). Insects may constantly move between areas in search of food or breeding partners or change activity overnight. Furthermore, the relationship between insects and bats may be more specific, in which each species of gleaned animalivores consumes specific insect species (Oliveira *et al.* 2015). Thus, the high number of insect species captured by light traps may have masked the relationship between bats and insect species composition. Analysis on each bat species, as has been performed for *Pteronotus parnellii* (Oliveira *et al.* 2015), may be more revealing. Plants can provide ripe fruit for several consecutive days, and are therefore a more predictable

food resource for frugivorous bats over time. Frugivorous bats are sometimes 'trap-liners' and can return to the same tree even when few fruits available. However, it is important to note that the relatively low role of food availability in the use of space by bats may also have been a consequence of the methods used for its quantification. Counting the number of plants with fruits may not reflect the number of fruits produced by plants. Light traps are not selective and may have sampled insect species that the gleaned bats do not hunt.

Overall, our study corroborates the hypothesis that primary consumers, such as frugivorous bats, are more influenced by the direct availability of food-providing plants in food webs, while secondary consumers, such as the gleaned animalivores species, are more influenced by the structural complexity of the vegetation (Rice *et al.* 1983, Jayapal *et al.* 2009, Jankowski *et al.* 2013). A novel finding of our study was the demonstration of how these predictor variables are related to each other and how they can directly and indirectly affect the structure and the diversity of bats in an Amazonian forest. The subtle variations in terrain elevation investigated here were related to the physical structure of vegetation, and the availability of fruits and insects consumed by bats. Terrain elevation was also an important variable in shaping the species composition of bat assemblages in the upper Rio Madeira and Chapada dos Guimarães National Park, located 780 km and

1430 km south of the Ducke Reserve, respectively (Koppe 2016, Bobrowiec & Tavares 2017). Being easy to measure, and globally available (Global Land Survey Digital Elevation Model, Global Land Cover Facility), it is therefore possible that terrain elevation can serve as a reliable predictor of bat-assemblage structure at local scales in other regions. The terrain elevation can be used as a substitute variable for vegetation structure and food availability (fruits and insects) when it is not possible to measure these variables during fieldwork.

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## DATA AVAILABILITY

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.9rb48c5> (Capaverde *et al.* 2018).

## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

FIGURE S1. Location of the Ducke Reserve and sampling plots in the RAPELD grid, Central Amazonia, Brazil.

FIGURE S2. Schematic illustration of the arrangement of mist nets, light traps for the sampling of insect availability, and the area for sampling of plants consumed by bats in each 250 m plot.

FIGURE S3. Abundance of the plants consumed by bats along the gradient in terrain elevation at Ducke Reserve.

FIGURE S4. Insect order abundance distribution along the gradient in terrain elevation at Ducke Reserve.

TABLE S1. List of bat families and species captured, with their respective guilds, abundances, and sampling plot occurrence at the Ducke Reserve, Central Amazonia, Brazil.

TABLE S2. Abundance, number of plots with record, and

range of plots with plant genera consumed by bats in the Ducke Reserve, Central Amazonia, Brazil.

TABLE S3. Abundance, number of plots with records, and the range of occurrence in the plots of insect order in the Ducke Reserve, Central Amazonia, Brazil.

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